

**A new Atlantic species of *Acanthemblemaria*
(Teleostei: Blennioidei: Chaenopsidae):
Morphology and relationships**

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Abstract.—*Acanthemblemaria johnsoni* is described from six specimens collected from shallow coral reefs at the north end of the Caribbean island of Tobago. The new species differs from all other Atlantic species of *Acanthemblemaria* by the combined spinous and soft dorsal-fin ray count of XXIV, 12–13. Evolutionary relationships of the new species are discussed in relation to the phylogeny of the genus proposed by Hastings (1990).

Shallow-water rotenone collections of fishes were made at the Caribbean island of Tobago in September 1990 by members of the Division of Fishes, National Museum of Natural History, and the Marine Fisheries Section, Tobago Fisheries, in a collaborative survey of the shorefishes of Tobago. Among the fishes collected were six specimens of the chaenopsid genus *Acanthemblemaria* that could not be identified using published descriptions and keys for the Atlantic members of the genus (Smith-Vaniz & Palacio 1974, Johnson & Brothers 1989). The small blennioid fishes of the genus *Acanthemblemaria* typically inhabit tubes in shallow-water coral reefs and are distinguished from other chaenopsids by having spiny cranial bones and two rows of teeth on the palatine (Stephens 1963, Smith-Vaniz & Palacio 1974). Our investigation of Atlantic *Acanthemblemaria* indicates that the six Tobago specimens represent an undescribed species.

The addition of the new species brings the number of known species in the genus to 17 (18 including “new species A” from

the eastern Pacific, see Hastings 1990); 10 in the tropical western Atlantic and 7 in the eastern Pacific, making *Acanthemblemaria* the most speciose genus in the family Chaenopsidae. The evolutionary history of the genus appears to show the influence of the emergence of the Isthmus of Panama, with two species pairs following the eastern Pacific-Caribbean distributional track (Hastings 1990). Using the characters examined by Hastings (1990), we hypothesize the phylogenetic relationships of the new species to other members of the genus and comment on its historical biogeography.

Methods

Counts and measurements generally follow Stephens (1963). Pore terminology is that of Smith-Vaniz & Palacio (1974) as modified by Johnson & Greenfield (1976) and Rosenblatt & McCosker (1988). All measurements were made to the nearest tenth of a millimeter using an ocular micrometer. Vertebral counts were made from radiographs. Tooth and gill-raker counts, as well as assessments of Hastings' (1990) os-

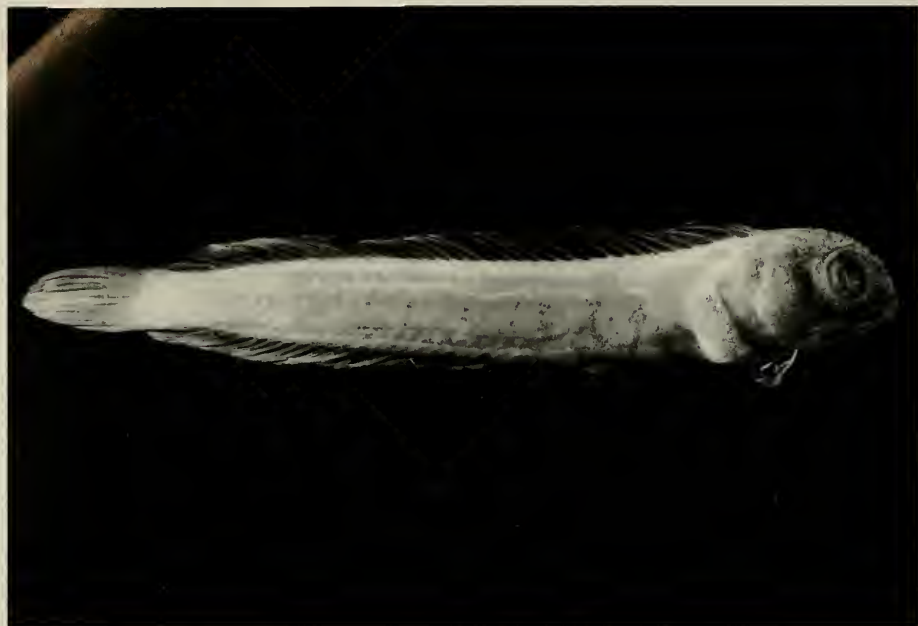


Fig. 1. *Acanthemblemaria johnsoni*, new species, holotype, USNM 317210, male, 24.0 mm SL, Tobago. Photograph by Carl Hansen, USNM.

teological characters, were made from a single cleared and stained specimen. Institutional abbreviations follow Leviton et al. (1985).

We reanalyzed Hastings' (1990) character matrix for *Acanthemblemaria* species including character states for the new species. The modified data set was analyzed using heuristic methods in PAUP 3.0. Multistate characters were treated as unordered and all characters were weighted equally.

Acanthemblemaria johnsoni, new species
Figs. 1, 2

Diagnosis.—An *Acanthemblemaria* differing from all other Atlantic members of the genus by its high number of dorsal-fin spines (XXIV) in combination with a low number of dorsal-fin soft rays (12–13, \bar{X} = 12.7), and in having blunt cranial spines, each spine covered with a simple, fleshy, tapering papilla. The new species differs from all Pacific *Acanthemblemaria* in having a low number of dorsal-fin soft rays in combination with several osteological fea-

tures (see “Relationships”), including equally spaced lateral ethmoid spines, the ventralmost spine not enlarged or separated from the others by a notch.

Counts and measurements in mm of holotype.—Dorsal fin XXIV, 13; anal fin II, 25; pectoral fin 13; pelvic fin I, 3; caudal fin 13 (7+6). Standard length 24.0; head length 6.0; head depth 4.0; upper jaw length 2.8; snout length 0.9; orbit length 1.8; least interorbital width 1.2; predorsal length 4.8; preanal length 10.9; caudal peduncle length 2.1; caudal peduncle depth 1.7; supraorbital cirrus length 0.8; pectoral fin length 2.3; longest dorsal-fin spine length 2.5.

Description.—Dorsal-fin spines XXIV, soft rays 12–13 (\bar{X} = 12.7); total elements 36–37 (\bar{X} = 36.7). Anal fin II, 24–25 (\bar{X} = 24.7). Pectoral-fin rays 13. Segmented caudal-fin rays 12–13 (\bar{X} = 12.8). Pelvic-fin rays I, 3. Vertebrae: precaudal 11; caudal 31–32 (\bar{X} = 31.8); total 42–43 (\bar{X} = 42.8).

Body elongate and slender as in other members of the genus. Similar in form to *A. greenfieldi* which lies in the middle of

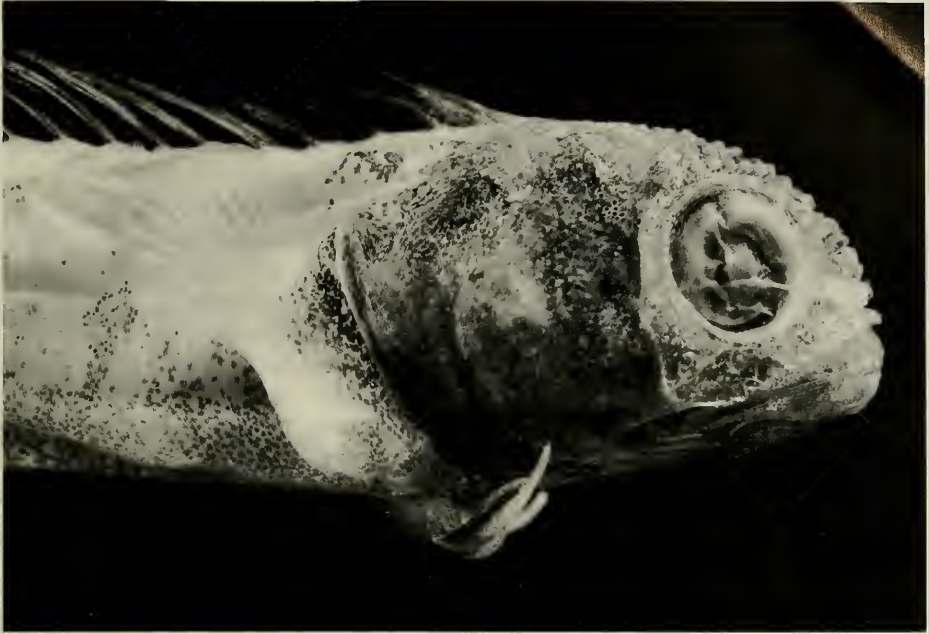


Fig. 2. (Top) *Acanthemblemaria johnsoni*, holotype, USNM 317210, photograph by Carl Hansen, USNM; (Bottom) head spines of *A. johnsoni* showing fleshy papillae.

the continuum between the very slender and elongate *A. paula* and *A. chaplini*, and the more robust forms such as *A. rivasi*. Head depth 4.8 to 6.0 in SL; head length 3.5 to 4.2 in SL.

Cephalic sensory pores: common 1; mandibular 4; preopercular 4; posttemporal 4; lateral supratemporal 3; median supratemporal 3; supraorbital 4; posterior infraorbital 3; anterior infraorbital 3; frontal 3–4; median interorbital 1; anterior frontal 1; nasal 1.

Vomerine teeth 6–8, arranged in a crescent. Palatine with two rows of teeth, approximately equal numbers in each row, 7–8. Premaxilla with outer row of 10–11 teeth. Antermost 4 teeth relatively large and incisiform. Remaining teeth conical with tips curving slightly posteriorly, teeth decreasing in size posteriorly. Inner band of minute, conical, posteriorly or medially curved teeth. Anterior region of dentary with approximately three rows of teeth: outer row with approximately 4 large, incisiform teeth, similar to those in premaxillae; inner band with approximately 4–5 small, conical teeth; a band of minute, posteriorly curved teeth lying between inner and outer rows. Posteriorly, a single row of approximately 5–6 conical teeth occurring on each dentary, teeth decreasing in size posteriorly. Gill rakers 2 + 6.

Anterior and dorsal region of head ornamented with dorsally or anteriorly directed blunt spines, each spine covered with a simple, tapering fleshy papilla (Fig. 2B). Posterior apex of spiny patch not extending more than half the distance between posterior rim of orbit and dorsal-fin origin. Supraorbital rim of each frontal bearing a row of anterolaterally directed blunt spines beginning slightly posterior to midline of orbit and continuing onto lateral ethmoid, which bears three to four spines. Posterodorsal rim of supraorbital flange smooth. Ventral edge of anterior region of first infraorbital with several ventrally directed blunt spines. Upper margin of first infraorbital also with ventrally directed spines. Second infraorbital with a patch of rugosities centrally

where infraorbital sensory canal opens in several places to surface; margins of second infraorbital smooth. Each nasal with six spines, four arranged in a semicircle around anterior nostril; a single spine projecting anteriorly from each nasal at the anterior symphysis. Nasal bones adjacent for most of their length, separating posteriorly, each limb bearing a dorsally directed spine near its posterior terminus. A row of spines on each frontal between orbits, separated by a median groove. Posterior to midorbit the interorbital rows of spines broadening into a diamond-shaped patch; weakest spine development occurring in posterior apex of this patch.

Dorsal-fin origin over posterior edge of preopercle. Membrane between spines and soft rays continuous between tips of adjacent elements, slightly incised. Each spine and soft ray curved posteriorly at distal end. Last spine approximately one half as long as first soft ray, creating a prominent notch at junction of spinous and soft portions of dorsal fin. Membrane between adjacent rays of anal fin also incised, each element in anal fin curving posteriorly at distal end. Last dorsal and anal rays connected by a membrane to caudal peduncle. Caudal fin slightly rounded, central rays longest. Membrane with notches between each ray creating a scalloped margin. Pectoral fin rounded with a weakly scalloped margin. Lower three rays thickened and bent such that distal ends curve dorsally. Central pelvic-fin ray longest. Membrane between pelvic-fin rays notched.

Supraorbital cirrus originating from dorsal membrane of eye. Cirrus usually a simple, distally tapering tentacle, rarely bifid (on right side of one male and the only female) or trifid (left side of the female); when divided, branching occurring near midpoint of cirrus. Anterior nostril surrounded by a sheath of skin which is surmounted at posterior region by a bifid or trifid cirrus. Supraorbital cirrus 1.3–2.3 in eye.

Color.—Color descriptions are based on

specimens preserved in alcohol. Background color light tan. Head darkly pigmented. Scattered melanophores on dorsal surface of head, denser in larger specimens. Pigmentation darkest on cheek and opercular region with a prominent dark, oval-shaped patch of melanophores just posterior to each orbit. Heavy pigmentation of head continuing onto anterior trunk in a diagonal band that begins at dorsal-fin origin and extends to dorsal edge of pectoral-fin base. Both supraorbital and nostril cirri with heaviest pigment at distal ends but bearing melanophores along entire length. Melanophores also found on dorsal region of orbital membrane around base of supraorbital cirrus. On underside of head, pigment concentrated on branchiostegal rays such that they appear almost black. Membrane between branchiostegals lighter in color. Indistinct transverse band across middle of lower jaw. In the female specimen, transverse band unpigmented. Anterior third of lower jaw and anterior portion of upper jaw lightly pigmented relative to rest of head.

Anterior two thirds of body barred, bars well developed in larger individuals, less distinct in smaller individuals. Anteriormost bar typically beginning above pectoral-fin base and posteriormost occurring near first dorsal soft ray. Each bar approximately as wide as distance between two or three dorsal-fin elements and darkest at lateral midline of body. Posterior third of body with few scattered melanophores, but otherwise unpigmented. On ventral midline, melanophores concentrated between pelvic-fin base and vent; darkest between pectoral fins. This pigment darkest in larger specimens and may not reach all the way to the vent in smaller specimens. Ventral midline pigment extending up sides of trunk between anal-fin origin and pelvic fins, forming dorsal extensions that are confluent with barred pattern on sides of trunk.

Pigment on dorsal fin concentrated on distal ends of, and membrane between, spines I through approximately IX. Pigment darkest on and between spines I-IV, melano-

nophores occurring along entire length of spines. Little or no pigment posterior to spine XVII or XVIII. Soft rays of dorsal fin unpigmented except for a few, faint melanophores along edges of some rays. Anal-fin pigment heaviest on spines I and II and continuing at least to ray 2 and sometimes to ray 15. Pigment heaviest on rays, but also scattered on membrane. Little or no pigment on anal fin posterior to ray 15. Single female specimen with no detectable pigment on anal fin. Caudal fin unpigmented except for faint melanophores along edges of some central elements. Pelvic fins with pigment on rays and membrane; medial rays darkest, outer rays lightest. Pectoral-fin base with even scattering of melanophores, slightly darker posteroventrally. Melanophores also occurring sometimes at proximal ends of fin rays, but central and distal regions unpigmented.

Color in life unknown.

Sex.—Individuals can be sexed based on genital morphology (Böhlke 1957). Males have a single papilla at the posterior margin of the anus whereas females have a papillar fringe surrounding the anus. There appears to be little sexual dimorphism in pigmentation or morphology, except for the lack of anal-fin pigmentation on the single female specimen. The small number of specimens, five males and one female, precludes conclusive statements regarding sexual differences.

Comparisons.—*Acanthemblemaria betinensis* and *A. greenfieldi* are the only other Atlantic species of *Acanthemblemaria* known to have 24 dorsal-fin spines (Smith-Vaniz & Palacio 1974). The modal number of dorsal-fin spines in *A. betinensis* is 23 ($\bar{X} = 23.2$) and 22 ($\bar{X} = 22.2$) in *A. greenfieldi* (Smith-Vaniz & Palacio 1974). *Acanthemblemaria betinensis* can be further distinguished from *A. johnsoni* by its dark background body coloration and by having two common pores versus only one in the new species. *Acanthemblemaria greenfieldi* can be further distinguished from *A. johnsoni* by its weakly developed cranial spines and

complexly branched supraorbital cirri. Like, *A. johnsoni*, *A. maria* and *A. rivasi* usually have 12 or 13 dorsal-fin soft rays, and *A. spinosa* sometimes has 13 (Smith-Vaniz & Palacio 1974); however, *A. maria* has 23 or fewer dorsal-fin spines, and *A. spinosa* and *A. rivasi* each has 22 or fewer dorsal-fin spines (Smith-Vaniz & Palacio 1974, Johnson & Brothers 1989). The remaining Atlantic species of *Acanthemblemaria* never have 24 dorsal-fin spines or 12 or 13 dorsal-fin rays, and can be further distinguished from the new species as follows: *A. medusa* has very weak development of cranial spines, is largely unpigmented, and has a very complex and highly branched supraorbital cirrus; *A. aspera* has sharp cranial spines, a highly branched supraorbital cirrus, and very little pigment on the body; *A. paula* has a very small but elongate body and sharp cranial spines; and *A. chaplini* has a highly branched and complex supraorbital cirrus, a very elongate body, and weak development of the cranial spines.

The blunt head spines of *A. johnsoni* are more similar to those of some eastern Pacific *Acanthemblemaria* species than to those of most Atlantic species. As noted below, *A. johnsoni* shares many features with most eastern Pacific *Acanthemblemaria*.

Relationships.—Hastings (1990) hypothesized phylogenetic relationships among 17 species of *Acanthemblemaria*. In general, his phylogeny (Hastings 1990: fig. 1) suggests that the western Atlantic species are cladistically primitive members of the genus, forming a succession of sister groups to a clade comprising primarily eastern Pacific species. Exceptions include a sister-group relationship between the eastern Pacific *A. castroi* and western Atlantic *A. rivasi* within the eastern Pacific clade, and a sister-group relationship between the eastern Pacific *A. exilispinus* and western Atlantic *A. betinensis* below the eastern Pacific clade. Following Stephens (1963), and using evidence from a preliminary parsimony analysis of all chaenopsid genera, Hastings (1990) considered *Ekemblemaria*

as the first outgroup for *Acanthemblemaria*. Hastings (1992a) provided an additional synapomorphy of those genera. The sister group of the *Acanthemblemaria* + *Ekemblemaria* clade was not clear from Hastings' (1990) study, and he constructed a hypothetical second outgroup for use in analyzing relationships within *Acanthemblemaria*. In a more thorough phylogenetic analysis of chaenopsids, Hastings & Springer (1994) suggested that the sister group of the *Acanthemblemaria* + *Ekemblemaria* clade is a group of seven genera that form two monophyletic groups: the "Chaenopsis clade," comprising *Chaenopsis*, *Lucayablennius*, *Hemiblemaria*, *Emblemaria*, and *Tanyemblemaria*, and the "Coralliozetus clade," including *Coralliozetus*, *Protemblemaria*, and *Emblemariopsis*. Although a single cladistically primitive genus from these clades has not been identified, *Emblemaria* and *Tanyemblemaria* appear to be cladistically primitive members of the *Chaenopsis* clade (Hastings 1992b), and *Protemblemaria* and *Emblemariopsis* may be primitive with respect to *Coralliozetus* (P. A. Hastings, pers. comm., July, 1995). In efforts to have a tangible second outgroup for analysis of relationships of *A. johnsoni* within the genus, we added character states for *Protemblemaria* to the data matrix. Although we recognize that further study of chaenopsid phylogeny is needed to test the appropriateness of using *Protemblemaria* as a second outgroup for *Acanthemblemaria*, we note that Stephens (1963) characterized *Protemblemaria* as having numerous primitive characteristics, and he believed it is the most primitive genus in the Chaenopsidae.

Character states of *A. johnsoni* for the 60 characters of Hastings (1990) are, in numerical order, as follows: 1, 2, 2, 0, 0, 1, 1, 0, 1, 0, 1, 2, 0, 0, 1, 1, 2, 0, 1, 2, 1, 1, 0, 1, 1, 1, 0, 1, 0, 0, 0, 0, 1, 0, 0, 1, 1, 0, 0, 1, 1, 2, 0, 0, 1, 0, 0, 0, 1, 0, 2, 2, 0, 2, 0, 0, 1, 0, 0, and 0. We coded character 52, the shape of the supraorbital cirrus, as state 2 (unbranched or rarely branched once near

tip). The single female specimen of *A. johnsoni* has one bifid cirrus and one trifid cirrus, and one male specimen has one bifid cirrus. The supraorbital cirri in all other specimens of the new species are simple. We coded character 53, the length of the supraorbital cirrus, as state 0 (one half to one orbital diameter) versus state 1 (less than or equal to one half the orbital diameter). The length of the supraorbital cirrus in *A. johnsoni* varies from less than one half the orbital diameter to greater than one half the orbital diameter, a condition intermediate between the two character states defined by Hastings (1990). Coding the length of the supraorbital cirrus in *A. johnsoni* as short (state 1) does not affect the topology of the tree. We coded character 54, the shape of the nasal cirrus, as state 2 (branched more than once). The nasal cirri in *A. johnsoni* are either bifid (state 1) or trifid (state 2).

Character states of *Protemblemaria* for the 60 characters of Hastings (1990) are: 0, 0, 0, 0, 0, 0, ?, 0, 0, ?, ?, 0, 1, 0, 0, ?, 0, ?, 0, 0, 0, 0, 0, 0, 1, 0, 0, 0, 0, 1, 0, 0, 0, 1, 0, 0, 0, ?, 0, ?, 2, 0, 0, 0, 0, ?, 0, 1, 0, 2, 0, 0, 2, 0, ?, ?, ?, ?, and 0. Most question marks indicate characters not present in *Protemblemaria* (e.g., head spines), but we coded two characters, 39 and 47, as “?” due to the presence of a condition that does not match any states defined by Hastings (1990). The vomer of *Protemblemaria* (character 39) has three teeth forming a crescent with a single tooth posteriorly, the shape of the patch being neither a crescent nor a circle; and *Protemblemaria* has a single ossified thread (vs. none or two) on the posterior inner margin of the pelvis (character 47). Coding those characters in *Protemblemaria* with a new state number rather than a “?” has no effect on tree topology.

Although we did not stipulate a transformational order for any of the 12 multistate characters in the analysis a priori as Hastings (1990) did for three features (his characters 2, 3, and 7), our PAUP analysis yielded the same relationships as those sug-

gested by Hastings (1990: fig. 1) for the 17 species of *Acanthemblemaria* he examined, regardless of whether we used *Protemblemaria* or Hastings' hypothetical taxon as the second outgroup. The advantage of using *Protemblemaria* is that only 12 of the 60 characters are coded as “?” (not applicable, or other than Hastings' states) versus 24 characters coded as “?” in Hastings' hypothetical second outgroup. Our phylogeny differs from Hastings only in the number of characters supporting some nodes (compare Fig. 3 and Table 1 with Hastings 1990: fig. 1 and Table 1).

Our study suggests that *A. johnsoni* is the sister group of a clade comprising *A. crockeri*, *A. balanorum*, *A. rivasi*, *A. castroi*, *A. macrospilus*, “new species A” of Hastings (1990), *A. hancocki*, and *A. stephensi* (Fig. 3), all of which are eastern Pacific taxa except *A. rivasi* and *A. johnsoni*. All eastern Pacific species except *A. exilispinus* are members of this clade, and herein we refer to species above *A. johnsoni* on the cladogram as the “eastern Pacific clade.” Derived features supporting a sister-group relationship between *A. johnsoni* and the eastern Pacific clade are as follows (character numbers correspond to those of Hastings 1990): (33)—ventral portion of metapterygoid not reaching anteriorly to ectopterygoid; (49)—a notch present at the juncture between the spinous and soft dorsal fins, the last spine less than one half the length of the first ray; (51)—membrane posterior to the dorsal and anal fins attached to the caudal peduncle; and (52)—supraorbital cirrus unbranched or rarely branched once near the tip. As noted in the description of *A. johnsoni* above, the supraorbital cirrus is occasionally bifid or trifid, but it is never highly branched in a pinnate or palmate manner as in most Atlantic *Acanthemblemaria* and the Pacific *A. exilispinus*. It is thus somewhat intermediate between the primitive, highly branched condition found in primitive *Acanthemblemaria* and the unbranched condition of most eastern Pacific species; our placement of *A. johnsoni* between these two groups is con-

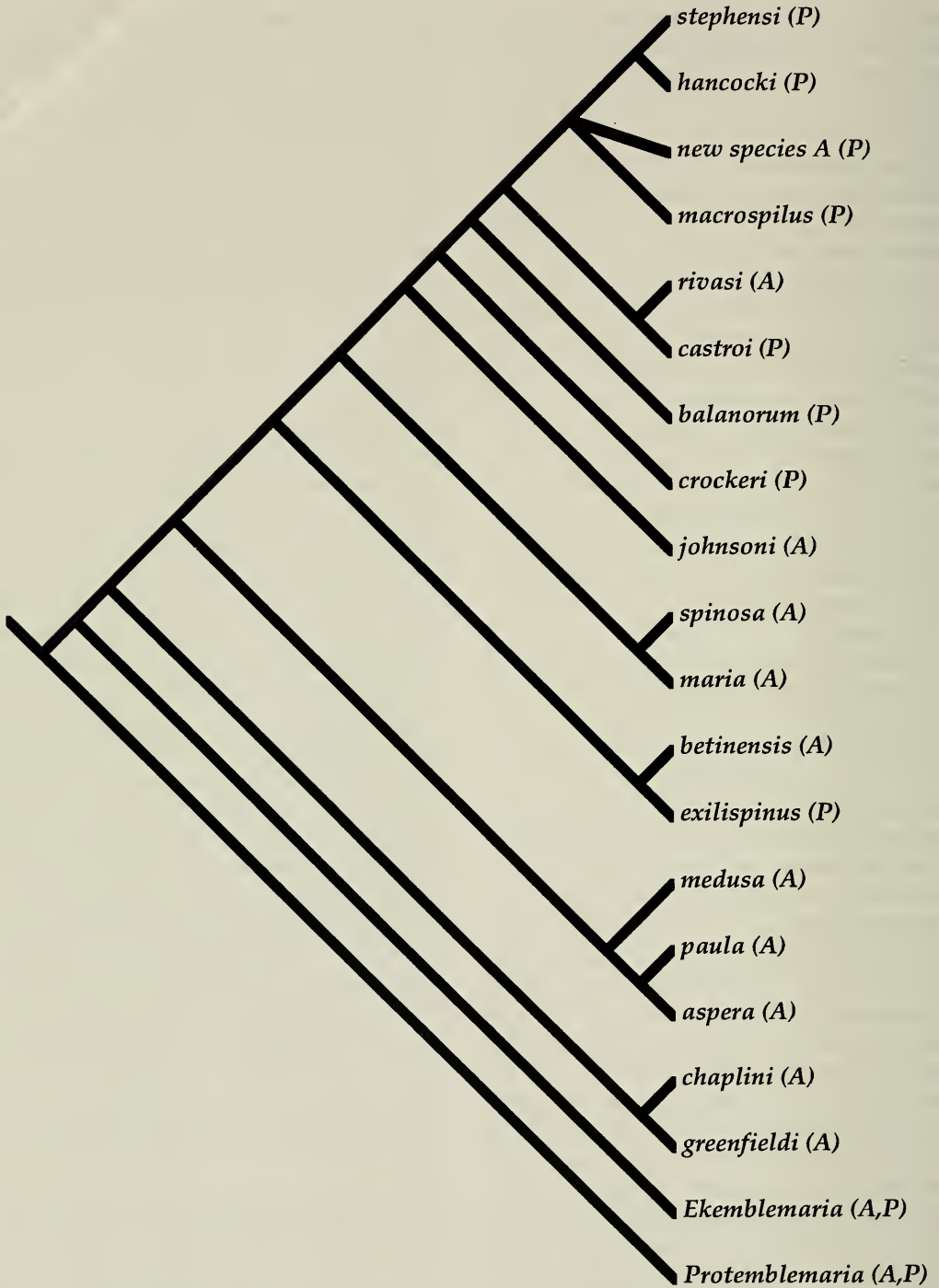


Fig. 3. Hypothesized relationships of *Acanthemblemaria* species. (A) = western tropical Atlantic; (P) = eastern Pacific.

Table 1.—List of apomorphic characters that support the hypothesized relationships among *Acanthemblemaria* species as depicted in Figure 3. For a definition of characters and states, see Hastings (1990: appendix table 1). Character states are given in parentheses. Ambiguous characters that support nodes when optimized using ACCT-RAN are indicated by an “*”.

Description of group	Apomorphic characters
<i>Acanthemblemaria</i>	6(1), 12(2), 34(2)*, 40(1)
<i>chaplini</i> + <i>greenfieldi</i>	44(1), 51(1), 55(1)
<i>medusa</i> + <i>aspera</i> + <i>paula</i> and above	2(1), 9(1)*, 19(1), 20(2), 25(1), 36(1)
<i>medusa</i> + <i>aspera</i> + <i>paula</i>	13(1), 23(1), 39(1), 52(1)
<i>aspera</i> + <i>paula</i>	34(1)*, 51(1), 57(1)
<i>betinensis</i> + <i>exilispinus</i> and above	1(1), 7(1), 15(1), 22(1), 26(1), 29(1)*, 34(0)*, 35(1), 37(1)*, 41(1), 42(0)
<i>betinensis</i> + <i>exilispinus</i>	12(1), 20(1), 56(1), 58(1), 60(1)
<i>spinosa</i> + <i>maria</i> and above	2(2), 14(1)*, 24(1), 28(1)
<i>spinosa</i> + <i>maria</i>	4(1), 5(1), 7(2), 27(1), 30(1), 37(0)*, 48(1)
<i>johnsoni</i> and above	29(0)*, 33(1), 49(1), 51(2), 52(2)
<i>johnsoni</i>	14(0)*, 16(1), 35(0), 42(2), 45(1), 57(1)
<i>crockeri</i> and above	11(0)*, 18(1), 31(1), 38(1), 39(2), 44(2)
<i>balanorum</i> and above	12(1), 20(1), 37(0)*, 43(1), 46(1), 47(1), 58(1)
<i>rivasi</i> + <i>castroi</i> and above	8(1), 50(1), 54(1)*, 56(1)*
<i>rivasi</i> + <i>castroi</i>	7(0), 10(1), 15(0), 17(1), 20(0), 32(1), 33(0), 37(1)*, 44(0)
<i>macrospilus</i> and above	38(0), 42(1)*, 59(1)
<i>hancocki</i> + <i>stephensi</i>	16(1), 53(1), 54(2)*

sistent with these data. The presence of a multiple-branched cirrus in *A. crockeri* is autapomorphic.

Acanthemblemaria johnsoni lacks the five derived features that unite the eastern Pacific clade (Fig. 3, Table 1): (18) an enlarged ventralmost lateral ethmoid spine that is well separated from others by a notch; (31) postorbital excluded from the posterior angle of the circumorbitals; (38) two rows of teeth on the ramus of the dentary; (39) vomer with two patches of teeth with a median hiatus; and (44) epineural bones (formerly epipleural ribs—see Patterson & Johnson 1995) present on all precaudal vertebrae and two or more caudal vertebrae. In *A. johnsoni*, lateral ethmoid spines are equally spaced, the ventralmost not separate; the lacrimal and postorbital both extend into the posterior angle of the circumorbitals; the ramus of the dentary bears a single row of teeth; the vomerine tooth patch is in the shape of a crescent; and epineurals are present on all precaudal vertebrae and sometimes on the first caudal vertebra.

Acanthemblemaria johnsoni has all of the derived features that diagnose the major clades leading up to the eastern Pacific clade (Fig. 3, Table 1) except characters (14) frontal with a central row of interorbital spines; (35) epihyal and ceratohyal suture complex, with seven or more interdigitations (both unite *A. betinensis* + *A. exilispinus* and above); and (45) fifth hypural ossified (equally parsimonious to hypothesize this condition as a synapomorphy of *A. betinensis* + *A. exilispinus* and above, or of *A. medusa* + *A. paula* + *A. aspera* and above). *Acanthemblemaria johnsoni* independently evolved (16) a continuous and straight row of lateral interorbital spines positioned well medial of the interorbital margin (a synapomorphy of *A. hancocki* and *A. stephensi*); and (57) anterofrontal pores fused into a single medial pore (a synapomorphy of *A. paula* and *A. aspera*, an autapomorphy of *A. spinosa*).

In summary, based on the phylogenetic data assembled by Hastings (1990), the affinities of the new species from Tobago clearly lie with the predominantly eastern

Pacific clade of *Acanthemblemaria* species. In addition to the characters listed above in support of this hypothesis, *A. johnsoni* is also more similar to eastern Pacific species in meristic features than to western Atlantic species. For example, a dorsal-fin count of XXIV, 12–13, is diagnostic for *A. johnsoni* relative to Atlantic species of the genus, but 24 dorsal-fin spines also occur in the Pacific *A. exilispinus* and *A. hancocki*, and is the modal count for *A. crockeri*, *A. macrospilus*, *A. balanorum*, and *A. stephensi* (Stephens 1963, Rosenblatt & McCosker 1988).

An analysis of the cladistic biogeography of the genus is beyond the scope of this study, but the phylogeny of species hypothesized by Hastings (1990) and expanded herein suggests a complicated biogeographical history. The initial radiation of the genus appears to have occurred in what is now the tropical western Atlantic, and, as noted by Stephens (1963), the primary radiation of the eastern Pacific species may have taken place since the last emergence of the Panamanian isthmus.

Within *Acanthemblemaria*, there are now three sister-group relationships pairing an Atlantic species with one or more eastern Pacific species (Fig. 3): *A. betinensis* and *A. exilispinus*, *A. rivasi* and *A. castroi*, and *A. johnsoni* and the eastern Pacific clade. Hastings (1990) noted that the distributions of *A. betinensis* and *A. exilispinus* are consistent with a hypothesis of allopatric speciation resulting from the emergence of the isthmus of Panama, and the same event could simultaneously have led to the division of *A. johnsoni* and the ancestor of the eastern Pacific clade. The ancestor of *A. rivasi* and *A. castroi* would not have been present at this time, but subsequent dispersal of that species to the Atlantic, possibly through an incompletely formed isthmus after the initial radiation of *Acanthemblemaria* in the eastern Pacific, could explain the phylogenetic affinities of *A. rivasi* with some of its eastern Pacific congeners. As noted by Hastings (1990), the distribution of the *A. rivasi* and *A. castroi* species pair,

Central America and the Galapagos, respectively, is unusual.

Acanthemblemaria johnsoni is presently known only from shallow reefs at the north end of Tobago, but the historical distribution of the ancestor of *A. johnsoni* and the eastern Pacific clade must have been different from the known distribution of *A. johnsoni* today. Optimizing Atlantic and eastern Pacific distributions of *Acanthemblemaria* species on the cladogram suggests that the ancestor of *A. johnsoni* and the eastern Pacific clade inhabited Atlantic waters. It is thus reasonable to assume that this ancestor was once found along the eastern coast of Central America and the northern coast of South America. Further sampling of these areas may reveal that *A. johnsoni* is not restricted to Tobago.

Etymology.—It is our pleasure to name this species for G. David Johnson who assisted in the collection of these specimens. He has made contributions to the systematics of a broad array of teleostean taxa (including *Acanthemblemaria*), and his knowledge of teleostean anatomy and phylogeny is inspirational.

Habitat.—The specimens of *A. johnsoni* were collected at large rotenone stations and thus were not observed in their natural habitat. Presumably *A. johnsoni*, like other members of the genus, inhabits the vacated tubes of invertebrates, such as polychaetes or sipunculids.

Distribution.—Known only from shallow-water reefs at the north end of the Caribbean island of Tobago.

Holotype.—USNM 317210, 24.0 mm male taken with rotenone from an area with rock, live coral, gorgonians, rubble, and numerous, large, vertical walls on a reef north of Charlotteville, on the east side of North Point, Tobago, at a depth of 4.5–12 m on 8 Sep 1990 by J. Williams and party.

Paratypes.—USNM 317211 (4, 19.5–25.5 mm; one 21.9 mm male cleared and stained). Same locality and collection data as holotype, USNM 317210.

USNM 319706 (1, 14.8 mm); Saint Giles

Islands, Saint Giles Island, Tobago. Collected with rotenone from a rocky bottom shelf with some live and dead coral, rock, and rubble, at a depth of 6–10.5 m on 12 Sep 1990 by J. Williams and party.

Other material examined.—*Acanthemblemaria aspera*, USNM 274944 and 276049; *A. balanorum*, USNM 299794; *A. chaplini*, ANSP 100887 and 100880; *A. crockeri*, USNM 299798; *A. greenfieldi*, USNM 321067; *A. hancocki*, USNM 299791; *A. maria*, USNM 317081; *A. medusa*, USNM 317077 and 329332; *A. paula*, USNM 308400 and 327611; *A. rivasi*, ANSP 119230 and 147649; *A. spinosus*, USNM 320858, 320812, and 317072; *A. betinensis*, SIO 71-262; *Protemblemaria bicirris*, USNM 200400 and UAZ 95-1-1 (C&S).

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